

**BIOLOGICAL STUDIES OF *PLAGIOMERUS DIASPIDIS* CRAWFORD, A  
PRIMARY INTERNAL PARASITE OF DIASPIDID SCALE INSECTS  
(HYMENOPTERA: ENCYRTIDAE: HOMOPTERA: DIASPIDIDAE)**

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**ABSTRACT**—Studies of *Plagiomerus diaspidis* Crawford indicate that it is a solitary internal parasite of *Diaspis echinocacti* (Bouché). When tested against third instar scales of six other species of diaspidid scale insects, the parasite was host specific and also exhibited ovipositional site preference, ovipositing in the prosoma and depositing eggs on the ventral surface of the scale body. Although thelytokous, males were produced by subjecting immature females to high temperatures (29.5°C or above). Male courtship is described, but copulation was not observed. As the male has an unusual habitus and the systematic placement of *Plagiomerus* is questionable, the male is described in detail. The taxonomic and biological relationships of the three described species of *Plagiomerus* are discussed.

The genus *Plagiomerus* Crawford consists of three described species: *P. diaspidis* Crawford, *P. cyaneus* (Ashmead) and *P. hospes* Timberlake. The latter species was described from material collected on Oahu, Hawaii, but Timberlake (1920) writes that the species was probably an immigrant from North America. Ferriere (1953) records *P. diaspidis* in Italy (on *D. calypteroides* Costa = *D. echinocacti*) and Trjapitzin (1968) reports that *Plagiomerus* sp. was accidentally introduced into the Soviet Union at Baku with its host *D. echinocacti*. Trjapitzin (1968) was unable to determine the identity of *Plagiomerus* sp. because of the brevity of the original descriptions and a lack of comparative material. There are also six female specimens in the USNM of an undescribed species of *Plagiomerus* taken on Taiwan from *Aulacaspis murryae* Takahashi.

The systematic placement of *Plagiomerus* is unsettled. Hoffer (1955) places it in the Cercobelini with *Cercobelus* Walker. According to Hoffer (1960) *Cercobelus* is characterized by a four-segmented funicle in both sexes, and the hosts are *Psyllopsis* spp.; *Plagiomerus* males have a two-segmented funicle and a banana-shaped clavus; females parasitize armored scale insects. Compere and Annecke (1961) note that the genera *Anabrolepis* Timberlake, *Habrolepis* Förster and *Adelencyrtus* Ashmead are related based on

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mandible dentition and presence of lamelliform setae on the apex of the female scutellum. Trjapitzin (1973) places *Plagiomerus* in the Habrolepidini, subtribe Habrolepidini, including the genera mentioned by Compere and Annecke, *Homalopoda* Howard, *Pseudhomalopoda* Girault, *Parahomalopoda* Girault and *Adelencyrtoides* Tachikawa and Valentine.

#### MATERIALS AND METHODS

*Plagiomerus diaspidis* was detected as a contaminant of an *Aphytis* nr. *linguaensis* Compere culture maintained on *D. echinocacti* in the University of California, Riverside, insectary. After isolation, *P. diaspidis* was reared in a one-hole sleeve cage on cactus pads (*Opuntia* spp.) infested with 3rd instar *D. echinocacti*. Pads were added to the culture weekly, and pads in the culture more than 1 month were discarded.

Material used in behavior studies was obtained by removing pads from the culture, examining the scales under a dissecting microscope and isolating parasitized scales in ¼ dram vials with a drop of honey added as nutrition. Daily observations were made for adult parasite emergence, and the age of each female parasite was recorded. Morphological studies on immature parasites were performed in several ways. Parasitized scales from the culture were removed from the pads, immersed in 30% ETOH for several hours and the scale bodies teased apart with forceps and dissecting needles. Next the material was mounted in glycerine or stained with acid fuchsin and mounted in Hoyer's medium. Permanent mounts were made by killing in 30% ETOH, running the specimen up through alcohol to 100% ETOH, through clove oil and mounting in Canada balsam.

Ovarian eggs were removed from 4 day old female parasites that had been continually deprived of hosts. Eggs were observed by killing the female parasite in 30% ETOH, holding the body with a pair of forceps and grasping the base of the ovipositor with another pair of forceps and tugging gently. In so doing the reproductive system was often removed intact. Next the ovaries were placed in acid fuchsin for several minutes, washed in distilled water and then slide mounted in glycerine.

Voucher specimens of the material studied have been deposited in the following institutions: Plant Protection Research Institute, Pretoria, South Africa; British Museum (Natural History); U. S. National Museum; Zoological Institute, Soviet Academy of Science, Leningrad; and the Canadian National Collection, Ottawa.

In the following discussion the term "scale" is intended to mean the scale cover and the scale insect body together.

#### RESULTS

##### Female search and oviposition behavior:

Female parasites lived up to 35 days. Three to five day old nulliparous parasites were released on cactus pads infested with *D. echinocacti* in all stages of development and observed under a dissecting microscope. Search of a seemingly non-systematic or random nature, characterized by antennal drumming of the substrate, pro-

ceeded immediately. Mature female scales, both gravid and ovipositing, were most attractive to the searching parasites; crawlers, white caps, and second instars were generally ignored. Second instar female and male scales seemed attractive to older *Plagiomerus* females that had been deprived of hosts for more than ten days after emergence, but after extensive examination with the antennae they were not attacked. Antennal drumming on the scale covers found to be attractive ranged from less than ten seconds to several minutes ( $n = 32$  observations). Females that had been allowed contact with hosts since emergence would often spontaneously abandon antennal drumming and move to another scale or begin grooming activity. Upon again coming in contact with the scale cover a second time, most females were observed to have little interest in it.

If the scale cover was found suitable for attack, the female moved off the scale, assumed a position perpendicular to a tangent to the cover margin, lowered her body and inserted the ovipositor shaft into the scale by a backward movement of the body (fig. 1). One to several insertions of the ovipositor into the scale body preceded oviposition. Sometimes the scale was abandoned after insertion of the ovipositor but before an egg was deposited. Females deprived of hosts for five to eight days after emergence oviposited in up to ten scales in rapid succession. Unoccupied scale covers were found to be more attractive to searching females than exposed mature scale bodies. A nulliparous female was observed to insert her ovipositor through an unoccupied cover, but eggs were not deposited.

Host feeding was noted in a few instances but was not an apparent prerequisite for oviposition. Feeding consisted of the female thrusting her ovipositor through the scale cover and into the scale body several times then backing up to feed on the exudate welling up at the point of ovipositor penetration.

#### Oviposition site preference and egg dispersion:

To determine female oviposition site preference several females were allowed to parasitize scales and egg position was tabulated. (Eggs were noted by the conspicuous stalk projecting through the host's integument—see below). Figure 2 indicates the position of 98 eggs with respect to four quadrants of the scale body. There was no significant difference between the number of eggs laid in quadrants one and four or two and three, suggesting that there was no bilateral oviposition site preference. There was a highly significant difference between the number of eggs laid in quadrants one plus four (69 eggs) and two plus three (29 eggs) ( $\chi^2 = 8.16$ ,  $p < 0.005\%$ ), indicating that females oviposited more frequently in the prosoma than in the pygidium.

Eggs were also scored with respect to the vertical, counted as





Fig. 1. Female *Plagiomerus diaspidis* ovipositing into *D. echinocacti*.

upper surface, midline and lower surface. Thus nine eggs were laid on the upper surface of the scale body, 21 eggs were laid on the midline and 68 eggs were deposited on the ventral surface of the scale body. All eggs were deposited near the lateral margin of the scale body. Combining the eggs scored as midline or above, a highly significant difference was noted between the number of eggs deposited above and below the midline ( $\chi^2 = 13.97$ ,  $p < 0.005\%$ ), suggesting that the female preferred to oviposit on the ventral surface of adult female scales.

Informal observations of the stock culture showed that only a single parasite emerged from each parasitized host. Several scales from the stock culture were dissected from the cactus pads during the period when new material was added when the parasite population was exceptionally high and numerous females were actively ovipositing. (Because population structure was such that distinct peaks were noted and adult emergence was largely synchronous, it was believed that these conditions approximated a highly competitive situation in nature.) A random sample of the scales removed and examined revealed that 38 scales had one parasite egg, 22 scales had two parasite eggs, 2 scales had three parasite eggs and 1 scale had four parasite eggs. The pads were then returned to the culture (because the scale population on the pad was high and many scales were still not parasitized). Examination of the host population from the same ovipositional episode a week later revealed numerous instances of more than one parasite larva in individual scales. However, in nearly two years of observation we did not notice more

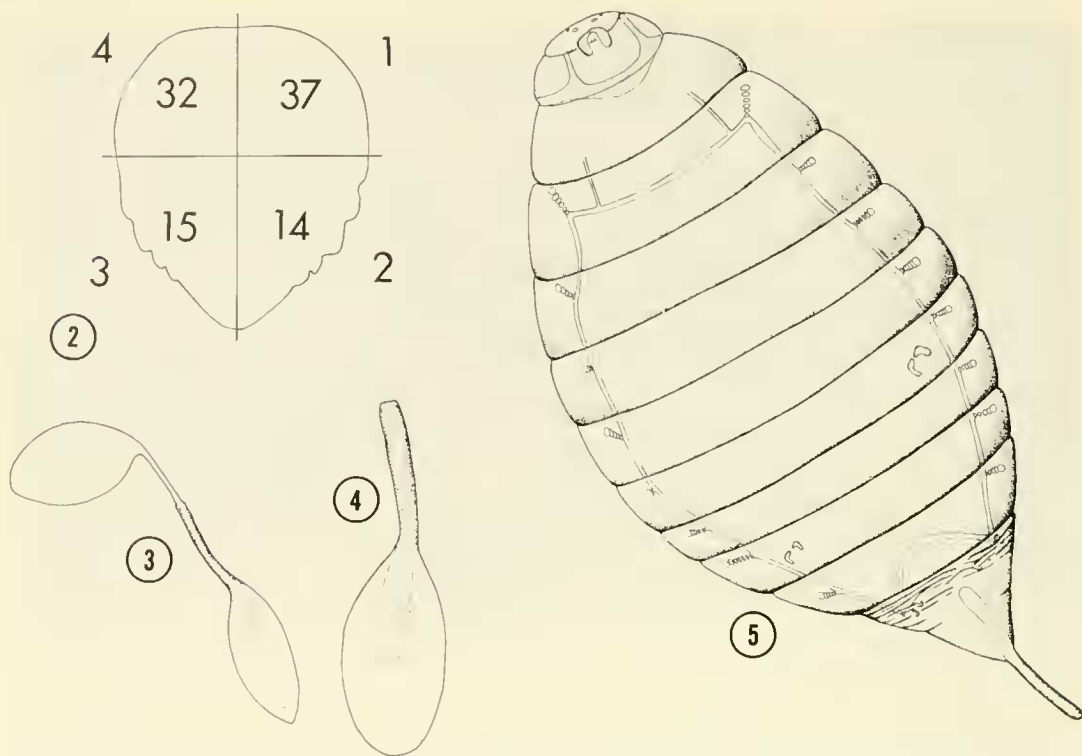


Fig. 2. Schematic diagram illustrating number of parasite eggs deposited in each quadrant of host body. (Quadrants indicated outside the body margin, number of eggs deposited inside body quadrant.) Fig. 3-5. *Plagiomerus diaspidis*. 3, ovarian egg. 4, deposited egg. 5, mature larva.

than one pupa develop or adult parasite emerge from an individual scale insect. Presumably larval combat occurs.

#### Immature development and stages:

The ovarian egg of *P. diaspidis* is encyrtiform (fig. 3). After deposition the bulb collapses at the stalk apex (fig. 4). The stalk of the deposited egg projects through the host integument and serves as an anchor for the egg body. The stalk is uniform in diameter and approximately half as long as the egg body. Eggs are the banded type with the aescopic plate reticulation pattern completely surrounding the stalk and forming a peninsula approximately halfway down the egg body (fig. 3, 4). The reticulation pattern is uniform, and the remainder of the chorion is smooth. Respiration is thought to occur through the stalk reticulation pattern.

The exact duration of egg incubation after oviposition was not determined but required one to three days at the temperatures indicated.

Larval development required seven to nine days at  $26.7^{\circ} \pm 1.5^{\circ}\text{C}$ . The mature larva (fig. 5) is 13 segmented, lacks setae and is attached to the host cuticle via the stalk. The anterior-most body segment of the larva bears two pairs of sensilla. Cast exuviae of earlier instars accumulate around the base of the stalk and as determined by the

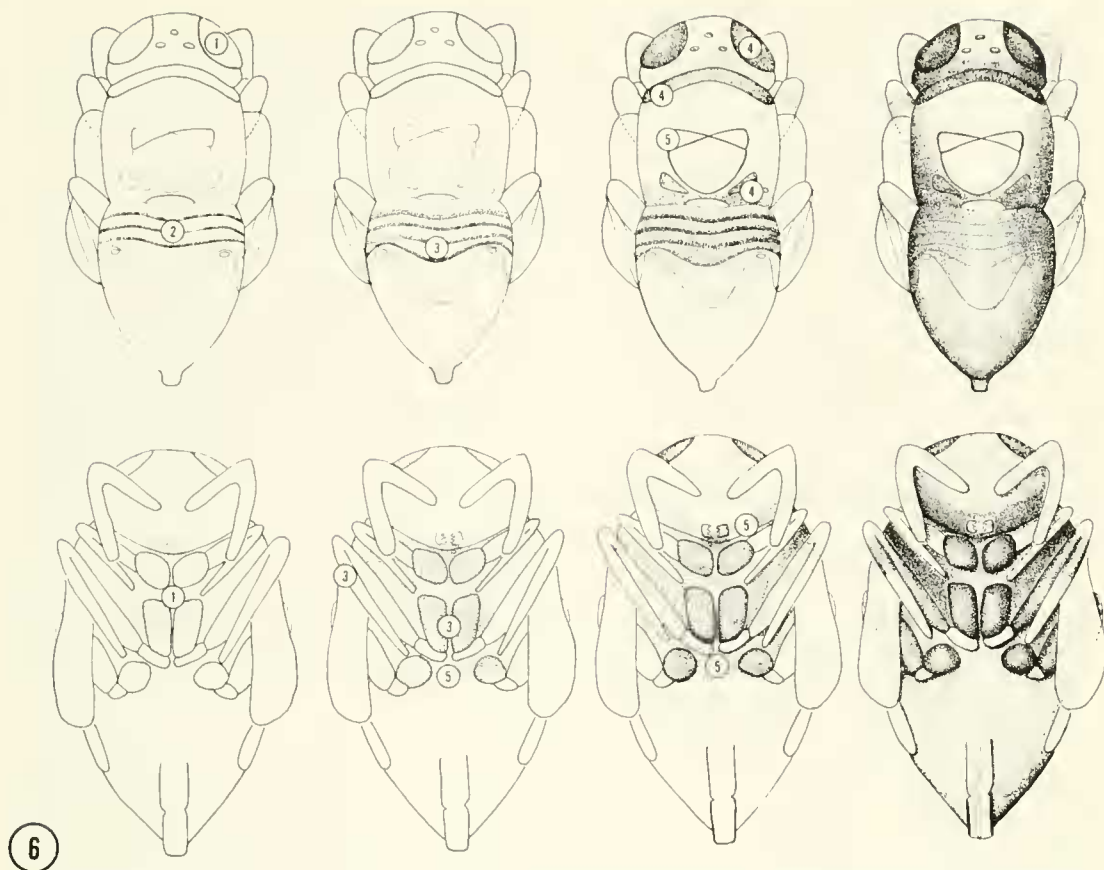


Fig. 6. Schematic diagram illustrating the sequential pattern of pupal pigmentation of *Plagiomerus diaspidis*.

number of mandibular exuvia *P. diaspidis* apparently has four feeding instars. The tracheole network is an open system with the spiracle aperture and tracheole diameter uniform throughout the system. The mature larva has nine pairs of spiracles on segments 4–12 and a parallel longitudinal tracheole system which connects transversely in segments four and twelve. Spiracles connect to the tracheoles via loosely spiraled taenidia.

The host's body contents are completely consumed by the parasite larva and only the transparent, parchmentlike host integument remains.

Initially, the prepupa becomes dorsoventrally flattened and transformed into a form with seven pairs of lateral lobes. The body color changes from pale white to light yellow, and meconial pellets are deposited on both sides about halfway between the anterior and posterior ends of the body.

The pupal stage lasts five to seven days. After assuming the pupal shape the body is translucent peripherally and white centrally. The sequential deposition of pigmentation is stereotyped and complicated (fig. 6, numbers indicate the order in which parts become pigmented).



Pigmentation begins with the compound eyes turning faintly pink and the mesopleuron and coxae turning dusky. Next, the posterior margins of terga one thru three become dusky. Shortly afterwards, the banding pattern appears on the middle and hind tibiae and the pleuron and coxae darken. Concomitantly, the posterior margin of tergum four darkens and the entire surface area of terga one thru three darkened (although the posterior margins remain noticeably darker). Later the compound eyes and ocelli turn red, and the pronotum and lateral margins of the propodeum become dusky. Next, there seems to be a general darkening of the body parts indicated above, but the head, dorsal region of the thorax and body appendages remain translucent or opaque. After considerable darkening of the parts mentioned above, the metanotum and thoracic notal sutures become dark. As the first and second sterna become dusky so do the gena and apical terga. Later the remaining sterna become uniformly dusky and the remainder of the thoracic notum (scutum and scutellum) darken. The antennae become dark shortly before emergence.

#### Adult emergence and host preference:

Adults emerged by chewing their way through the host's integument and the scale cover. Newly emerged female parasites were quiescent for two or three days or at least ovipositional activity was not observed during that period.

Studies were conducted with adult parasites to determine the host specificity of *P. diaspidis*. Individual five day old female parasites were placed in one pint mason jars with lemons or potatoes infested with third instar scales of the following species: latania scale (*Hemiberlesia lataniae* (Signoret)), California red scale (*Aonidiella aurantii* (Maskell)), purple scale (*Lepidosaphes beckii* (Newman)), yellow scale (*Aonidiella citrina* (Coquillett)), dictyospermum scale (*Chrysomphalus dictyospermi* (Morgan)) and oleander scale (*Aspidiotus nerii* Bouché), in addition to *D. echinocacti*. Ten replicates of each group were used and each experimental cell was maintained at  $26.7^{\circ} \pm 1.5^{\circ}\text{C}$  and  $50 \pm 10\%$  RH for ten days, then the females were removed. Cells were then maintained at the temperature and relative humidity indicated for an additional 15 days, and then the cells were examined for parasite development, activity or emergence. Parasite progeny emerged only from cactus scale. Examination of the scales did not reveal sting marks or indication of parasite-induced moribund scales other than for *D. echinocacti*. When host-deprived female parasites were offered the above mentioned scale species and then observed under a dissecting microscope, the parasites drummed the scales but oviposition or drilling was not observed in any scale species except *D. echinocacti*.

Production of males, courtship behavior and descriptive notes:

Field recoveries of *P. diaspidis* from *Opuntia* sp. infested with *D. echinocacti* at Irvine, California by Walter White revealed that encyrtid males were associated with *P. diaspidis* females. Two collections made by White during August showed males were present in low numbers (less than five males per several hundred females). However, in collections made at the same locality during other times of the year males of what was provisionally thought to be *P. diaspidis* were not recovered. As we knew that males of other thelytokous species of parasitic Hymenoptera produced males when subjected to high temperatures, the following experiment was conducted. Females were allowed to oviposit at 26.7°C and immatures were incubated at 32°C for the entire duration of development. In addition a control group was used in which eggs were deposited, hatched and immatures developed at 26.7°C.

All adults of both groups were female. These females were allowed to oviposit in cactus scale, and their  $F_1$  progeny developed at 80°F. All  $F_1$  progeny of the heat-treated parental generation were males; all progeny of the parental generation subjected to 26.7°C were females.

Studies to establish the exact temperature at which the sex shift occurred suggested that 29.5°C was apparently the critical temperature, but because of temperature fluctuations ( $\pm 1.5^\circ\text{C}$ ) this is only an approximation.

To determine the duration of exposure responsible for the temperature-induced shift, eggs were deposited by females at 26.7°C and then incubated at 32°C. Pads were removed from the high temperature cabinet during the early and late larval stages, prepupa and pupal stages. Only parasites subjected to high temperature during their entire development produced male progeny. Further studies indicated that the temperature-sensitive period was restricted to the pupal stage and that this is the period during which ovarian development occurs.

To determine male functionality, pairs of males and females were placed in quarter dram vials and observed with a dissecting microscope. Courtship behavior of the males resembled that of another encyrtid (*Comperiella bifasciata* Howard), but copulation was not observed. Males approached quiescent females and when one came within 8–15 mm of a female he began to sway from side-to-side while still approaching her. When the male's head was approximately two to three mm from the female's gaster, he would stop, begin to vibrate his antennae slowly, and attempt to touch the female's wings (folded over her gaster), or possibly the gaster itself, near the pygostyle with his antennal clubs. Female response to this behavior was either to



remain quiescent or move quickly. If the female moved, the male attempted to chase the female for a distance of six to eight cm but was eventually evaded. If the female remained quiescent while the male attempted to antennate the female's gaster or wings, after several seconds of this behavior the male would slowly move into a face-to-face position with the female. Male movement to a face-to-face position was such that his body was oriented with his head nearest the female and as he moved laterally the longitudinal axis of his body approximated a perpendicular to a line tangent to the closest point to her body. Concomitantly the antennae of the male still vibrated and there was some side-to-side swaying. When the male assumed a face-to-face position the female invariably moved away quickly. The above observations were made for males and females of ages ranging from newly emerged to senescent. In no instance was copulation observed, but this is not to infer males were non-functional. Rather, it suggests that the conditions for copulation were not appropriate.

The male resembles the female in habitus, but differs by having a five-segmented antenna (1, 1, 2, 1) (fig. 7) with scape slightly dilated ventrally, funicular segments nearly anelliform and a banana-shaped club longer than all other segments combined. The apex of the scutellum bears two long, non-lamelliform setae. The pygostyli are situated just anterior to an imaginary transverse line bisecting the gaster, and all sterna are mesally setose. The mandible is four toothed (fig. 11); maxillary-palpus four segmented (fig. 9), labial-palpus three segmented (fig. 10), and the genitalia are as shown (fig. 8).

#### DISCUSSION

Taxonomically, *Plagiomerus* is puzzling. Crawford (1910) designated *P. diaspidis* type-species from material collected in New Mexico (host, *D. echinocacti*). Subsequently, Girault (1915) indicated that Ashmead's (1888) *Comys cyanea* from Florida was in fact a *Plagiomerus* (as determined by P. H. Timberlake). Later Timberlake (1920) described a third species, *P. hospes*, from material taken on Oahu, Hawaii. Material in the USNM indicates that *P. diaspidis* has been recovered in Maryland (on *H. lataniae*), Texas (on *D. echinocacti*), Washington, D.C. (on *D. echinocacti*), Florida ("Scale on cactus", *D. echinocacti*), Virginia (on *Chionaspis americana* Johnson), México (*D. echinocacti*) and Colombia (on *Clovastis* sp.). *P. cyaneus* has been recovered from México, (Morelos—on *H. diffinis* (Newstead); Matamoros and Cuernavaca—hosts unknown) and Trinidad (on *Ceroplastes cirripediformis* Comstock). *Plagiomerus hospes* has been recovered on Bermuda ("Scale on Melia") and Trinidad (on *D. bromiliae* (Kerner)). Timberlake (1920) reported that *P.*

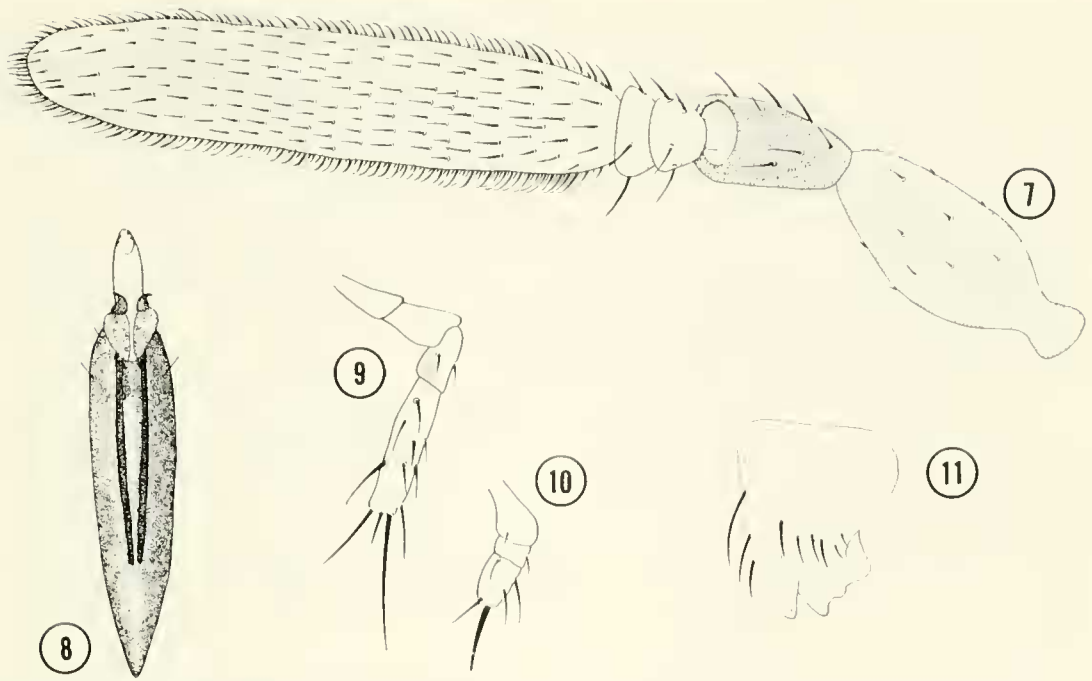


Fig. 7-11. *Plagiomerus diaspidis*. 7, male antenna. 8, male genitalia. 9, maxillary palpus. 10, labial palpus. 11, male right mandible, inner aspect.

*hospes* was probably thelytokous. Males of *P. cyaneus* are unknown, but several males identified as *P. diaspidis* were reared from *H. lataniae* by H. S. McConnell during 1928.

The characters used to separate the three species are variable. *Plagiomerus hospes* is distinguished from the others on the basis of the narrow lamelliform setae on the apex of the scutellum and the relatively short black band at the base of the middle tibia. Girault (1915) reports that *P. cyaneus* can be distinguished from *P. diaspidis* on the basis of the former species having funicular segments three and four white and the mesoscutum more hairy. Ashmead (1888) describes *P. cyaneus* on the basis of a unique female whose host is unknown. Dozier (1926) redescribed *P. cyaneus* from material he reared on Puerto Rico.

Study by one of us (GG) of the material in the USNM and additional material reared from *D. echinocacti* collected in California suggests that there can be variation in the characters used by others to separate *P. cyaneus* from *P. diaspidis*, namely the number of mesoscutal setae and antennal coloration. There also seems to be some variation in the width of the apical scutellar setae. However, because males of *P. cyaneus* are not known and the males of *P. diaspidis* produced did not mate, it is difficult to determine the reproductive status of the species involved. It seems undesirable to synonymize *P. cyaneus* and *P. diaspidis* at this time, although such a decision may be justified when the species are better known. Per-

haps an appreciation for species limits may be obtained by critical examination of immature stages, development and female behavior.

In a comprehensive analysis of encyrtid egg and larva morphology, Maple (1947) reported that encyrtid eggs were of three types: banded, unbanded and intermediate. In Maple's classification *P. diaspidis* eggs are banded. Maple also noted that size, shape, composition and extent of banding varies among species but is consistent within a species. His observations are consistent with the findings for the population of *P. diaspidis* studied.

Encyrtid larvae are classified as having closed or open tracheal systems. Closed systems form a loop within the body, and the open systems bear two or four caudal spiracles. Larvae that hatch from unbanded and intermediate egg types are apneustic; larvae that hatch from banded eggs are metapneustic. According to Maple (1947) metapneustic larvae remain attached to egg shells "so that the spiracles are in position to gain contact with the air-bearing structures of the egg proper."

*Plagiomerus diaspidis* remains attached to the egg shell throughout larval development, and mature larvae have nine pairs of spiracles. It is not known whether all pairs of spiracles are functional, but this seems questionable because of the taenidia which connect the spiracle to the tracheole are loosely coiled. Maple also notes that encyrtid larvae have cephalic branches at the point of union with the main trunk and two were noted in *P. diaspidis*.

The genetic mechanism responsible for the sequential deposition of pigmentation and its significance have not been studied in the parasitic Hymenoptera. However, informal studies by one of us (GG) have revealed that the pattern is constant in several species. Unknown is whether this constancy is a species or population phenomenon. The pattern is constant in *P. diaspidis* from California although genetic contact between individuals of the same generation of a population is restricted because *P. diaspidis* is thelytokous. The observed uniformity in the sequential pattern may suggest a functional necessity or a position effect may be influencing the pattern. Critical comparative study of pupal pigmentation in *Plagiomerus* may provide insight into the problems of delimiting species.

It is interesting to note that *P. diaspidis* was reared from *H. lataniae* in Maryland and *C. americana* in Virginia. It was not possible to obtain progeny from any scale species except *D. echinocacti* in the present study. This suggests perhaps that populations of *P. diaspidis* have adopted different host exploitation strategies in different areas.

Preferring to oviposit in the prosoma may indicate that nourishment is more easily obtained there because the third instar female has her prosoma filled with eggs. Feeding would conceivably be



more difficult in the pygidial area. Preference for a ventral egg deposition site may afford more protection for the stalk and aeroscopic plate. Undetermined as yet, however, are the modalities used to perceive front from rear and top from bottom of the scale body.

Production of males is noteworthy. Studies with other members of the Encyrtidae (Wilson, 1962; Wilson and Woolcock, 1960; Flanders, 1945), Signiphoridae (Quezada *et al.* 1973) and Trichogrammatidae (Bowen and Stern, 1966) have also shown that male chalcidoids can be produced with high temperatures. We hypothesize that the genetic manipulation of sex determination by high temperatures is not a laboratory artifact and that it is probably widespread in the parasitic Hymenoptera and that it has some adaptive advantage in that the otherwise thelytokous population produces males for genetic recombination during environmentally adverse periods. In so doing, a population may maximize its genetic fitness while not overtaxing a limited resource (superfluous males feeding on hosts).

#### REFERENCES

- Ashmead, W. H. 1888. Descriptions of new Florida chalcids belonging to the subfamily Encyrtinae. *Entomol. Amer.* 4:15-17.
- Bowen, W. R. and V. M. Stern. 1966. Effect of temperature on the production of males and sexual mosaics in a uniparental race of *Trichogramma semifumatum* (Hymenoptera: Trichogrammatidae). *Ann. Entomol. Soc. Amer.* 59: 823-834.
- Compere, H. C. and D. P. Annecke. 1961. Descriptions of parasitic Hymenoptera and comments (Hymenopt.: Aphelinidae, Encyrtidae, Eulophidae). *J. Entomol. Soc. S. Afr.* 24:17-71.
- Crawford, J. C. 1910. Three new genera and species of parasitic Hymenoptera. *Proc. U. S. Natl. Mus.* 38:87-90.
- Dozier, H. L. 1926. Notes on Porto Rican scale parasites. *Puerto Rico Dept. Agr. J.* 10:267-281.
- Ferriere, C. 1953. Encyrtides palearctiques (Hym. Chalcidoidea) nouvelle table des genres avec notes et synonymies. *Mitt. Schw. Entomol. Gesell.* 26:1-45.
- Flanders, S. E. 1945. The bisexuality of uniparental Hymenoptera, a function of the environment. *Amer. Nat.* 79:122-141.
- Girault, A. A. 1915. Some new chalcidoid Hymenoptera from North and South America. *Ann. Entomol. Soc. Amer.* 8:272-284.
- Hoffer, A. 1955. The phylogeny and taxonomy of the family Encyrtidae (Hym., Chalcidoidea). *Acta Mus. Natl. Pragae.* 11:1-21.
- . 1960. A revision of the Czechoslovak genera of the subfamily Encyrtinae with a reduced number of funicle segments (Hymenoptera, Chalcidoidea). *Acta Faun. Entomol. Mus. Nat. Pragae.* 15:93-119.
- Maple, J. D. 1947. The eggs and first instar larvae of Encyrtidae and their morphological adaptations for respiration. *Univ. Calif. Publ. Entomol.* 8:25-122.
- Quezada, J., P. DeBach and D. Rosen. 1973. Biological and taxonomic studies

- of *Signiphora borinquensis*, new species, (Hymenoptera: Signiphoridae), a primary parasite of diaspine scales. *Hilgardia*. 41:543-604.
- Timberlake, P. H. 1920. Descriptions of new genera and species of Hawaiian Encyrtidae (Hymenoptera), II. *Proc. Entomol. Soc. Hawaii*. 4:409-437.
- Trjapitzin, V. A. 1968. Review of the encyrtid fauna of the Caucasus. *Horae Soc. Ent. Union, Soviet*. 52:43-125. (Trudy Bessoy. Entomol. Obshtsh.) (In Russian).
- . 1973. Classification of the parasitic Hymenoptera of the family Encyrtidae (Chalcidoidea). Part II. Subfamily Encyrtinae Walker, 1837. *Entomol. Rev.* 52:287-295.
- Wilson, F. 1962. Environmental influences in sex determination in the Hymenoptera. *Nature*. 195:728-729.
- Wilson, F. and L. T. Woolcock. 1960. Temperature determination of sex in a parthenogenetic parasite, *Ooencyrtus submetallicus* (Howard) (Hymenoptera: Encyrtidae). *Austral. J. Zool.* 8:153-169.